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Foraging behavior of red foxes *Vulpes vulpes schrencki* utilizing human food in the Shiretoko National Park, Hokkaido

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Abstract. The utilization of human food (provisions) by red foxes, *Vulpes vulpes schrencki*, in the Shiretoko National Park was investigated to clarify the significance of begging behavior in a natural habitat. An analysis of 736 scats showed that foxes ate prey, such as rodents, insects, fruits, birds and deer, mainly in relation to their seasonal availability. The tendency to depend on a single dietary component increased in the latter half of the tourist season, when many tourists fed foxes, and was lower during the non-tourist season and the first half of the tourist season. The monthly variation in the utilization of provisions did not correlate with availability, and was negatively correlated with the increase in other single dietary components during the tourist season. During the non-tourist season, when relatively little natural food was available, foxes expended great energy to obtain provisions. It is concluded that red foxes in the Shiretoko NP, utilize provisions as a secondary food supply. Such food could be critical for them, however, in order to compensate for the lack of their major natural food resources at certain times of the year.

Key words: begging behavior, food habits, foraging behavior, provisions, *Vulpes vulpes schrencki*.

Red foxes, *Vulpes vulpes,* have a wide ranging diet, enabling them to survive in various environments. They are also flexible in their foraging behavior, changing to cope with the variation in the availability of each food item, as determined by their distribution, and abundance. One example of their flexibility is the development of begging, appearing in front of humans and waiting for them to provide food.

In heavily human-influenced habitats, scavenging enables foxes to access the abundant food source in the form of human waste, begging allows access to additional supplies actually given by people. In England, for example, it is well known that some urban residents actually feed foxes (Macdonald 1987),

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and in some cities in Hokkaido, Japan, foxes beg for food (Watanabe 1996). Hence, begging for food is a profitable strategy in areas inhabited by people. Of particular interest, however, is that foxes in more natural habitats also develop this strategy. In the Shiretoko National Park (Shiretoko NP), one of the most famous natural ecosystems protected in Japan, red foxes have been observed begging for food since 1970 (Tsukada 1994, Watanabe and Tsukada 1996). Tsukada (1994) indicated that begging was acquired by foxes through interactions with humans during their early lives, however, neither the factors which lead foxes to beg, nor the influence of the development of begging behavior on the utilization of natural food, have been clearly understood.

In this study, seasonal changes in the frequency of begging, and its relationship to human and natural food availability, were analyzed in order to clarify the importance of begging by foxes living in natural habitat.

Materials and Methods

1. Study Area

The study was conducted in the Shiretoko NP, eastern Hokkaido (Fig. 1), where the mean annual temperature is about 6°C and precipitation is 1100 mm, with winter snow depths reaching 1-2 m in lowland areas. The park is visited by 15 million tourists every year. This intensive study was conducted along the main tourist road in the park, the Shiretoko Park Road. This road has two

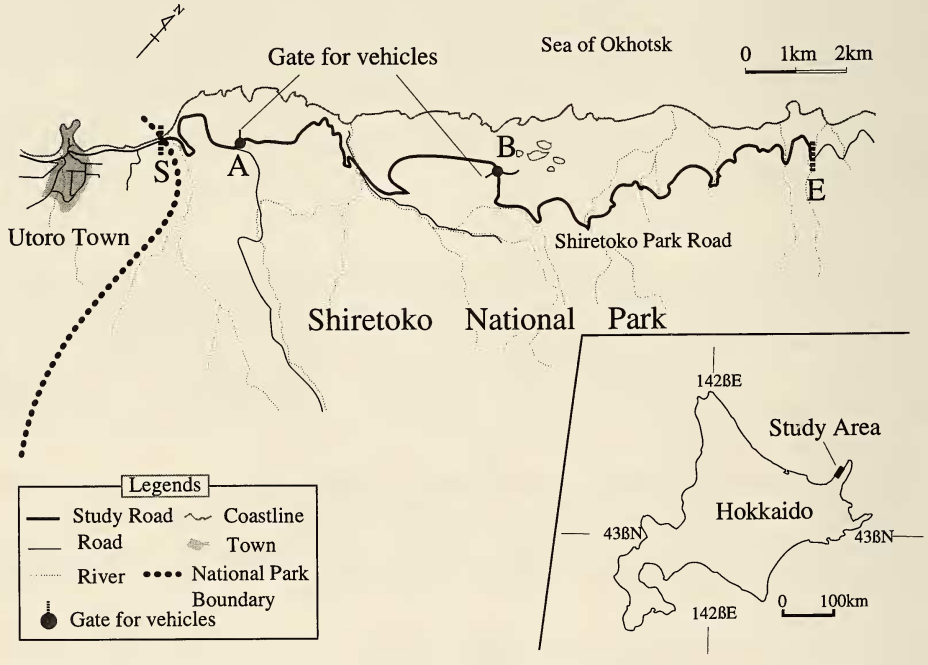

Fig. 1 Map of the study area.

gates, which are closed during winter. Gate A is open from May to November, enabling tourists to visit the south-west section of the road, and Gate B is open from June to October, enabling tourists to reach Point "E" (Fig. 1). The vegetation of the area is comprised of mixed broad-leaved and coniferous forests, with an admixture of the wild cherries, *Prunus ssiori* and *Prunus sargentii*, and lianes, such as the Tore vine, *Actinidia arguta*, and the wild grape, *Vitis coignetiae*, which occur at the edge of the forest.

2. Capturing and Identification of Foxes

From 1992 to 1994, forty three red foxes (♂18, ♀25) seen begging for food were captured in the study area, and fitted with individually identifiable colored ear tags (Allflex 25, Allflex New Zealand Ltd.). Foxes were classified into two age groups: juveniles (<1-year-old; ♂7, ♀11) and adults (≥1-year-old; ♂11, ♀14), by the degree of tooth wear (Harris 1978). Females which were rearing pups during June and July 1993 and 1994 were identified by the development of their nipples.

3. Begging for Food

Begging was defined as "appearing on or along a road in order to obtain food which might be given by humans". Practically, the following criteria were used to identify incidents of begging:

1) a fox appeared on or along the road during the day time when many tourists were likely to be about; and

2) a fox stayed in a position where people in their vehicles could notice them.

Observations were carried out from a car while driving the approximately 20-km-long Shiretoko Park Road (from "S" to "E" in Fig. 1) during the periods from June to October in 1993 and 1994, when both gates were open. This period is henceforth referred to as "the tourist season" and the remainder of the year as "the non-tourist season". The 20 km journey was made once every two hours from 07 : 00 to 17 : 00, on two weekdays each month (a total of twenty four trips). For each fox, its frequency of begging each month was calculated by the equation: the number of trips in the month, when begging was observed, divided by the total number of trips in the month with the exception of some juvenile foxes in 1994 which were not individually identified. In addition, the average number of juvenile foxes observed begging per kilometer of the total length of the trips, was calculated for each month in 1993 and 1994.

4. Fecal Analysis

Fox scats, deposited along the Shiretoko Park Road, were collected every month from April 1994 to February 1995, except for December 1994 (sample sizes: April 169, May 100, June 129, July 114, August 39, September 9, October 60, November 89, January and February 36; total 736). After taking samples for parasitological inspection, scats were preserved in a mixture of 1% formalin and 0.3% Tween 20, then sterilized by heating at 70°C for more than eight hours. Samples were then washed through a 0.1 mm mesh sieve. Undigested

items, identified by naked eye, or under a microscope, were weighed, after drying, to the nearest 1 mg. These items were first identified as "animal", "plant" or "other", then divided into broad categories, such as mammal, bird, reptile, fruit, or roughage (non-fruit vegetable matter), and then further classified into 17 narrow categories including all major food items of foxes in eastern Hokkaido (Abe 1975, Yoneda 1982). All items obtained from people were classified as "human food", or "provisions". The percentage occurrence and percentage weight of each food category were calculated (an adjustment for weight lost for parasitological inspection was made). The percentage occurrence of a category shows the relative frequency of that category in all fecal samples. The percentage weight of the same category shows its weight relative to the total weight of all categories.

Previous studies have usually multiplied the dry weight of food items by a coefficient of digestibility in order to estimate the amounts of food actually consumed (Goszczyñki 1974, 1986, Yoneda 1982, Jedrzejewski and Jedrzejewski 1992). In this study, however, the coefficient of digestibility of provisions and other food categories could not be obtained, thus such estimations were not feasible. Therefore, the dietary components of foxes were mainly traced by percentage occurrence. As this method is prone to the bias of under-estimating small food items (Kruuk 1989), we compared percentage occurrence to the results of percentage weight.

5. Estimation of Food Abundance

The availability of the major food sources of foxes in eastern Hokkaido, such as rodents, birds, insects and fruits (Abe 1975, Yoneda 1982), were estimated by the following methods, every month from April to November in 1994.

Rodent abundance was estimated from the number of individuals captured using 25 live traps baited with oats set for three days each month and checked every morning. Traps were set 10 m apart at four sites along the road. The number of rodents captured, excluding recaptures (released after clipping their toes) was recorded, and the number per 100 trap-nights was calculated to provide an index of rodent abundance.

Insect abundance was estimated from the number of terrestrial species collected in 20 baited pitfall traps (7 cm diameter, 13 cm height). Traps, one meter apart along trap lines set perpendicular to the road at four sites in the forest, were set for two days each month. The mean number of insects captured at all sites in each month was calculated and used as an index of abundance.

The relative abundance of fruit was estimated from the numbers of fallen ripe fruits. Forty seven *A. arguta* and *V. coignetiae* vines were selected along the road through the study area, and the numbers of ripe fruit on each vine were monitored. A decline in the number of fruit, after the maximum number was reached, was considered to reflect the availability of fallen fruit. The proportion of fallen fruit, in a given month, was calculated for each vine by the equation : (decrease in fruit numbers in a given month)/(maximum number of

fruit). The average proportion of fallen fruit from the 47 vines was used as an index of relative fruit abundance.

Bird abundance was estimated, based on the work of Nakagawa (1985), and Matsuda (unpubl.). From Nakagawa's (1985) description of the Shiretoko avifauna, and its seasonal change, the monthly species composition of birds in the study area was estimated. Seasonal variation in numbers of each species, was calculated from Matsuda (unpubl.), who censused the numbers of different species of birds in the same study area during the 1992 and 1993 summers (June and July), and the 1993 and 1994 winters (January and February). Matsuda's summer and winter numbers were used as monthly numbers for each species from April to November, and from December to March, respectively. The total number of all species of birds in each month was calculated by summation of the estimated number of each species of bird occurring in the month. This was used as an index of avian abundance.

The availability of provisions was estimated from the number of vehicles passing along the Shiretoko Park Road, because preliminary observation showed that most foxes were fed by tourists traveling by car or coach. Abundance was expressed as the number of vehicles met per minute by investigators on the whole park road in June-October in 1993 and 1994, and on the south-west of the road, from Gate B, during May and November of each year.

For the purposes of this paper, March to May are defined as spring, June to August as summer, September to November as autumn, and December to February as winter.

Results

1. Seasonal change in the frequency of begging during the tourist season

Thirty foxes (20 adults and eight juveniles in 1993; 15 adults and one juvenile in 1994, with some observed in both years) were observed begging for food a total of 557 times. There was no significant difference between the sexes, or between females in differing reproductive conditions, in the mean frequency of begging (Table 1).

Table 1. Frequency of food begging by adult foxes are compared between sexes or between reproductive conditions of female foxes. Mean with SE are given. Sample sizes are shown in parentheses.

	1993	U-test	1994	U-test
Adult males	0.16±0.04(n=8)	ns	0.13±0.02(n=4)	ns
Adult females	0.23±0.04(n=12)	ns	0.15±0.02(n=11)	ns
		ns		ns
Female in reproductive condition	0.23±0.04(n=9)	ns	0.14±0.03(n=6)	ns
Female in non-reproductive condition	0.22±0.07(n=3)		0.19±0.02(n=4)	

ns: statistically non-siginificant ($p>0.05$)

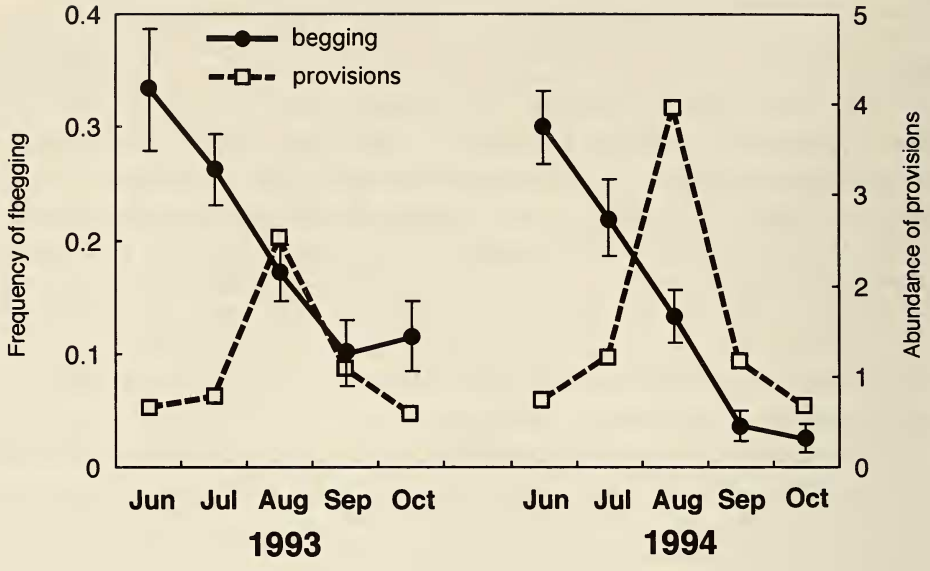

Fig. 2 Monthly variation in the frequency of begging by adult foxes (solid line with circles), and in the abundance of provisions (broken line with squores) in the study area.

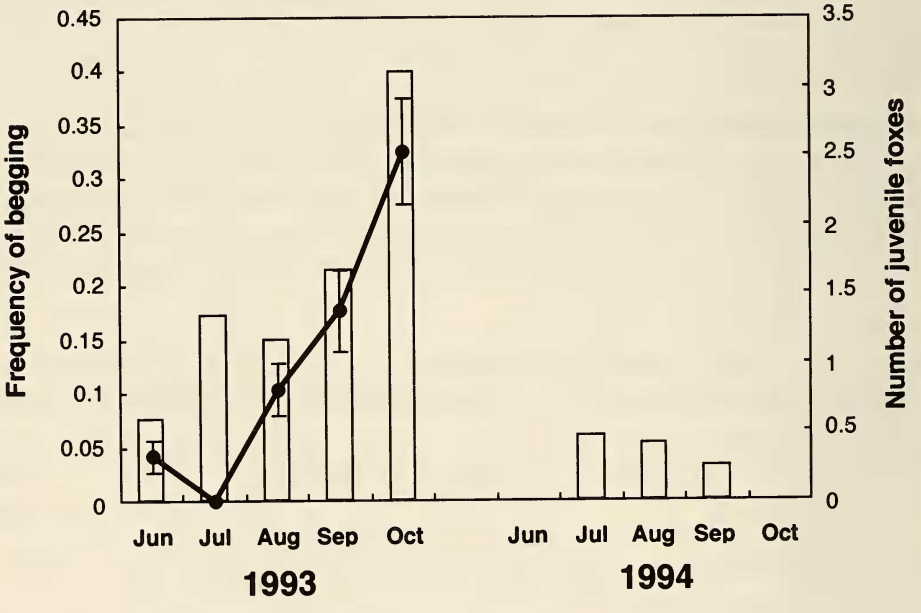

Fig. 3 Monthly variation in the frequency of begging by eight juvenile foxes in 1993 (solid line and circles) and in the average number of juvenile foxes begging per km in 1993 and 1994 (histogram).

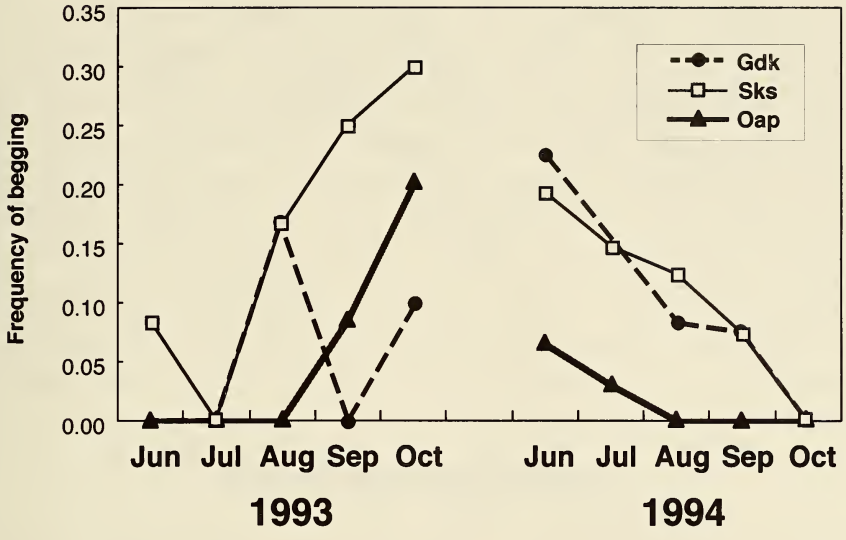

Fig. 4 Monthly variation in the frequency of begging by three foxes born in 1993.

The frequency of begging by adult foxes varied both between and within years. Among the 12 adults which were observed begging in both 1993 and 1994, the mean frequency of begging was significantly higher in 1993 (0.27 ± 0.03 *SE*) than in 1994 (0.15 ± 0.02 *SE* : Wilcoxon sign rank test, $p < 0.01$). In both years, however, adults were found to beg most in June and least in autumn (Fig. 2). This pattern of seasonal change was consistent in both years ($r^s = 0.96$, $p < 0.06$, $n = 5$).

The availability of provisions also varied between and within years. The mean abundance of provisions was significantly lower in 1993 (1.12 ± 0.32 *SE*), than in 1994 (1.55 ± 0.55 *SE* : Wilcoxon sign rank test, $p < 0.05$). It increased in summer, peaked in August, and decreased in autumn in both years. Surprisingly, the frequency of begging did not correlate with the availability of provisions.

As with adults, the mean frequency of begging by juvenile foxes also varied within the year, however, monthly fluctuations were not in phase with adults ; it was, for example, lower in summer and higher in autumn, while the reverse occurred in adults in 1993 (Figs. 2 and 3). In 1994, however, juveniles showed little begging behavior in autumn, and the number of juveniles begging per km was significantly lower than in 1993 (Wilcoxon sign rank test, $p < 0.05$; Fig. 3). Three young foxes born in 1993, also remained in their natal range throughout the 1994 study period. Their seasonal frequency of begging differed noticeably from that in 1993, and was highly correlated with that of other adult foxes ($r = 0.91$, $p < 0.05$; Fig. 4, cf. Fig. 2).

2. Food habits and food availability

Fecal analysis revealed that in terms of perctage occurrence, six food items ranked highest : roughage, rodents, insects, fruits, birds, and deer. Although roughage (consisting of dry twigs, dry leaves and grasses) occurred most frequently in feces, it was assumed to have been accidentally included in samples when collecting them, or that it had been swallowed with other food by the foxes, because it had not been listed as a staple food in previous fox studies (Abe 1975, Misawa 1979, Yoneda 1982, Kondo *et al.* 1986). Therefore, roughage was excluded in the following analysis. Five of the highest ranking dietary components by weight were : fruits, rodents, insects, deer and birds, which together accounted for 71.0% of the total weight of feces. Hence, the five major foods of Shiretoko foxes, both by percentage occurrence and by percentage weight, were rodents, insects, fruits, birds and deer. Provisions appeared in 11.8% of all fecal samples and accounted for 4.3% of total fecal weight (Table 2).

Table 2. Annual diet composition of fox feces in the Shiretoko National Park (n=736).

Food categories	Occurrence (%)	Weight (%)
Rodents	40.1	12.2
Insects	40.1	11.7
Fruits	26.5	29.5
Birds	22.0	7.7
Deer	16.7	9.9
Fishes	9.5	6.2
Other mammals	5.7	2.5
Unidentified	4.2	1.6
Soil	4.1	5.1
Earthworms	3.4	4.3
Other animals	2.3	0.8
Reptiles	2.2	0.6
Shellfishes	0.5	0.2
Crustcea	0.3	0.1
Fungi	0.3	<0.1
Roughage	44.6	3.3
Human foods	11.8	4.3

The composition of the diet was found to vary with the seasons. The greatest range of food categories found in feces occurred in April, May and June. The range then decreased until September, increased again in October and November, and decreased once more in January and February (Fig. 5). From May to November, just one food category occurred in more than 50% of scats each month. The percentage occurrence of the most frequently occurring category, each month, increased from May to November (with the exception of September, when the sample size was very small ; Fig. 5). Thus, the tendency to depend on a single dietary component increased from spring to

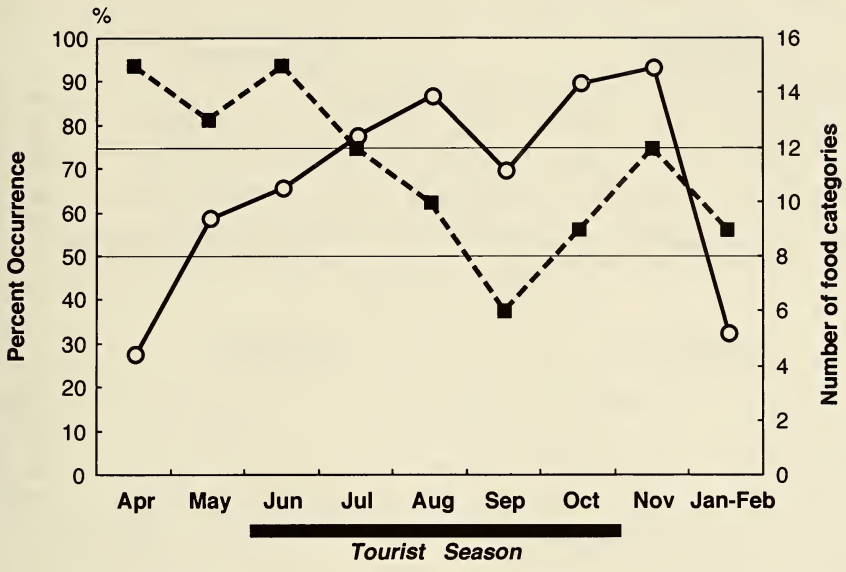

Fig. 5 Seasonal variation in the number of food categories occurring in feces (broken line with squares) and the percent occurrence of a food category showing the highest value each month (solid line with circles).

autumn, and decreased in winter.

The utilization of main food categories also changed seasonally. Fruits, such as *A. arguta, V. coignetiae* and *Prunus* spp., occurred most in autumn, with *A. arguta* in particular, accounting for 87.9% of the total weight of fruits taken. The seasonal variation in both percentage occurrence and percentage weight of fruit in fox feces was correlated with the change in their relative abundance (occurrence: Kendall's $\tau=0.68$, $p<0.05$; weight: Kendall's $\tau=0.58$, $p<0.05$; Fig. 6A).

Rodents included the northern red-backed vole, *Clethrionomys rufocanus*, and the grey red-backed vole, *C. rutilus*, and two endemic species of field mice *Apodemus speciosus* and *A. argenteus*. Voles occurred in 91.8% of scat samples containing rodents, and accounted for 90.2% of their total weight. Rodents occurred mostly in May, although the highest percentage by weight was in April (Fig. 6B). The abundance of rodents increased sharply from June to August, reaching a peak in October, yet there was no correlation with percentage occurrence in feces (Kendall's $\tau=-0.36$, $p>0.05$), although there was a negative correlation with percentage weight (Kendall's $\tau=-0.71$, $p<0.05$; Fig. 6B).

Insects available to foxes included Hymenoptera, Coleoptera, Orthoptera, and various larvae. Coleoptera in particular occurred in 91.8% of scats containing insects, and accounted for 96.4% of their total weight. Most insects occurred in samples collected during summer (Fig. 6C), with their percentage occurrence (Kendall's $\tau=0.81$, $p<0.05$; Fig. 6C) in scats correlated with their

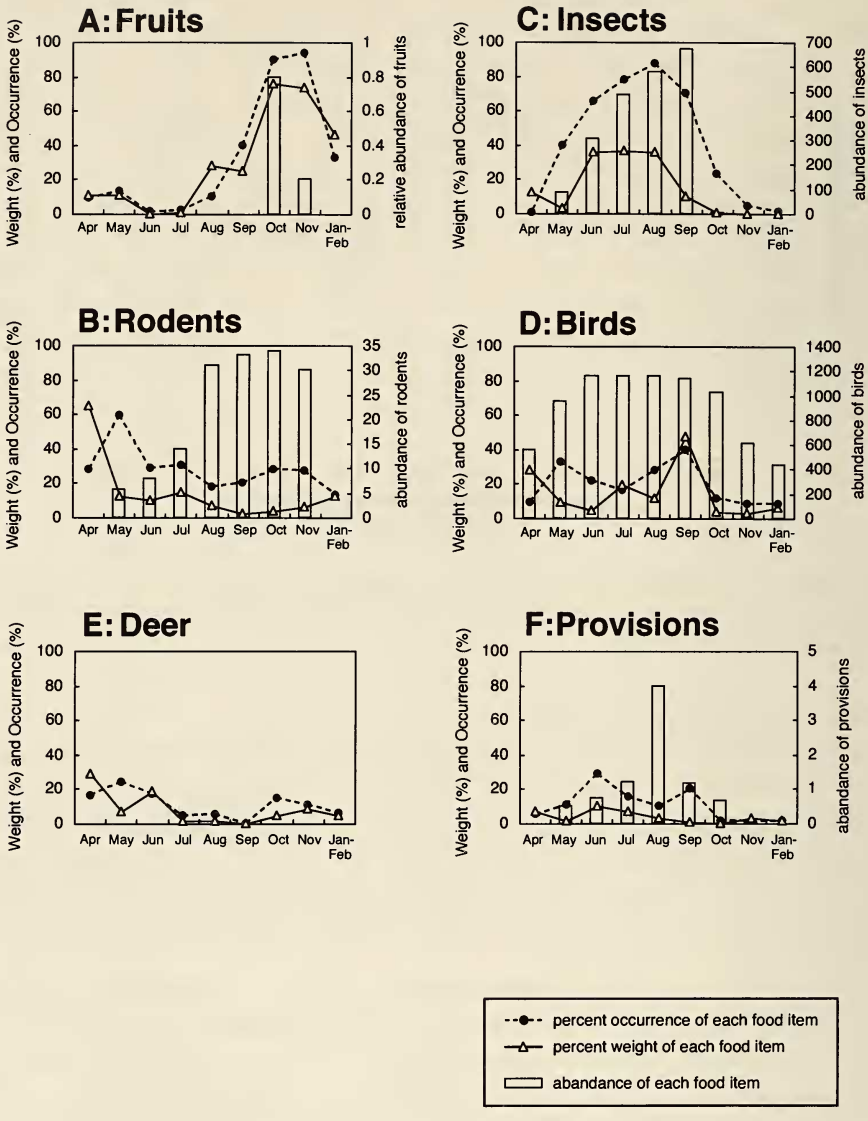

Fig. 6 Seasonal variation in the weight and occurrence of six dietary components and their abundance in the study area.

availability. The percentage weight, however, did not correlated with their availability (Kendall's $\tau=0.52$, $p>0.05$).

Birds were most abundant in May and September, however, neither their percentage occurrence nor their percentage weight in scats correlated with their abundance (occurrence: Kendall's $\tau=0.42$, $p>0.05$; weight: Kendall's $\tau=-0.99$, $p>0.05$) (Fig. 6D). A few pieces of egg shell were present in samples from May to July.

Sika Deer, *Cervus nippon*, occurred more frequently during April, May and June than in other months (Fig. 6E). In June, a few calf hooves were present in samples.

Provisions occurred most frequently during the tourist season, in spring and summer, peaking in June (Fig. 6F), and less frequently during the non-tourist season. During the tourist season, provisions included plastic materials, paper, aluminum foil, and corn. The frequency of begging by adult foxes during this season, correlated with the percentage weight (Kendall's $\tau=1.0$, $p<0.05$, n=5), but did not correlated with the percentage occurence of provisions (Kendall's $\tau=0.6$, $p>0.05$, n=5). This is probably due to the small sample size in September when begging was unexpectedly scarce. During the tourist season, provisions identified in fox scats were mostly composed of food given by people to begging foxes. The availability of provisions during the tourist season peaked in August, but did not correlate with either the percentage occurrence or the percentage weight of provisions in scat samples (occurrence : Kendall's $\tau=-0.14$, $p>0.05$; weight : Kendall's $\tau=-0.24$, $p>0.05$; Fig. 6F). The percentage occurrence of provisions in scats each month was found to be negatively correlated with the percentage occurrence of the most frequently occurring food during the tourist season ($r=0.96$, $p<0.01$), and showed a similar tendency in relation to the number of food categories, although the correlation was not significant in this instance, perhaps because of a potential bias in September due to the small sample size (Fig. 5, Fig. 6F).

During the non-tourist season, provisions occurred most in April and May, and household scraps were observed in 64% of feces counting all provisions.

Discussion

Begging by red foxes did not differ between the sexes, or between adults in differing reproductive conditions, thus indicating a general similarity in feeding strategies. This is in agreement with data on the food habits of hunted foxes from other countries, which also indicated that males and females had similar diets (Englund 1965, Sequiera 1980).

The difference in the frequency of begging, between juvenile and adult foxes changed seasonally. The frequency of adults begging decreased in autumn in 1993 and 1994, but the frequency of juveniles begging increased only in autumn 1993. Juvenile foxes were probably fed by their parents until they were 13 weeks old, or until July or August, and they gradually began to feed themselves (Nakazono 1994). In general, juveniles have inferior hunting skills during their first autumn, therefore, they tend to depend on more easily accessible food than adult foxes (Englund 1969, Sargeant *et al.* 1984). This would explain the increase in the frequency of begging among juveniles from spring to autumn in 1993, and furthermore, by the following year, 1994 (by when they had become more skillful hunters), three of those same juveniles from 1993 showed the same seasonal change in begging frequency as other older adults.

What was unexpected, however, was a reduction in the frequency of

begging by juvenile foxes from summer to autumn 1994. In October and November 1994 the fruit biomass of *A. arguta* was higher than in an average year (Matsuda pers. comm.), not surprisingly the readily available fruits dominated the diet of the foxes, occurring in 86.6% of scats (n=149). This was significantly higher than 1993 (33.8%, n=157 ; $\chi^2=88.5$, Fisher's exact $p<0.001$; Tsukada unpubl.). Thus, unlike in autumn 1993, in autumn 1994 juvenile foxes were easily able to depend on these fruits, their abundance probably explaining the decrease in begging in autumn 1994.

The seasonal change in the frequency of begging by adult foxes was similar in both 1993 and 1994. If this change was dependent on food abundance, it should have been positively correlated with changes in the abundance of provisions in each year. Such a correlation, however, was not observed. Furthermore, adults begged less frequently in 1994 than in 1993, whereas conversely provisions were more abundant in 1994 than in 1993, suggesting that there was no relationship between frequency of begging by adults and the availability of provisions. Why didn't begging frequency correlate with either seasonal or annual variation in the abundance of provisions?

According to Calisti *et al.* (1990), and Doncaster *et al.* (1990), the diet of red foxes varies in relation to food availability. The foxes in the Shiretoko NP study area tended to prefer one food category in each season. Such seasonal switching of preferred foods and main food categories is likely to be dependent on their availability. Food availability, however, can be broken down into two important aspects : abundance and ease of acquisition.

Food items such as fruits and terrestrial insects are easily obtainable, thus their availability is directly correlated with abundance. In fact, foxes in the study area chose these foods in relation to their abundance. On the other hand, the availability of active prey, such as live rodents and birds, is dependent on both their abundance and on their ease of acquisition. Rodents and birds were consumed by foxes but not in direct relation to their abundance.

During springs when ground cover, such as snow and grasses, were scarce, and hence rodent vulnerability was high, rodents were eaten frequently (Yoneda 1983, Jedrzejewski and Jedrzejewski 1992). Birds were eaten most during the migration seasons (April and September ; Matsuda pers. comm.), and during the nesting season (May to July), indicating that they were most intensively predated when most vulnerable. The utilization of deer by foxes increased from April to May (the period of highest mortality ; Kaji pers. comm.) ; it was also common in June, the peak birth period for deer on Shiretoko (Yabe 1995). Thus, rodents, birds and deer, major items in the diet of foxes on Shiretoko, were utilized depending on their vulnerability.

Adult foxes were easily able to obtain provisions during the tourist season. Even juvenile foxes, with inferior foraging skills and still mostly dependent on their parents for food, were able to obtain food from people. Therefore, the availability of provisions is considered to be directly correlated with its abundance. The utilization of provisions by foxes in the tourist season, however, did not depend on their availability. In fact, fecal and behavioral analyses

indicated that utilization of provisions was strongly dependent on the utilization of other food items, probably based on their availability. Indeed, the utilization of provisions was negatively correlated with the frequency of the primary dietary component during the tourist season.

A low contribution of a principle dietary component indicates the low availability of any particularly palatable prey. Such deficiencies tended to occur during April, May and June, and also during January and February. During these periods, foxes broaden their diet to include less preferred prey, such as shrews, insectivorous small mammals (Macdonald 1977) which occur in feces only during April (weight: 1.8%; occurrence: 5.3%) and May (weight: 0.3%; occurrence: 1.0%). Of particular interest is that provisions were found more frequently in feces during April, when the park road was closed, than in October, indicating that foxes made lengthy excursions to human residential areas up to 13 km from the locations where feces were collected. Admittedly, such excursions were made by some foxes which begged for food even during the non-tourist season (Tsukada 1994). These particular individuals expended a great deal of energy to obtain provisions when major natural foods were scarce.

Given that foxes in the Shiretoko NP showed no notable inclination towards provisions, even during the tourist season, when the availability of provisions was highest, it appears that provisions were utilized mainly as a secondary food source, when more palatable and preferred natural foods were absent or less abundant. This observation is not unique, as Englund (1965), and Lucherini and Crema (1994) also observed that some human waste were used as a secondary food source in other natural habitats.

The major, previously reported, fox prey items are small rodents, hares and rabbits, wild fruits and berries, insects, and birds (Ables 1975, Lloyd 1980, Sequiera 1980), all of which fluctuate in their abundance, and thus in their availability to foxes. It must be vitally important for foxes to meet the temporal shortages in their major prey. Provisions are generally available year round wherever human activity occurs. Furthermore, in Shiretoko NP, many outdoor recreationists visit natural areas inhabited by foxes and make provisions available to foxes. Provisions seem, therefore, less preferable than natural foods, but provide an alternative when natural foods are in short supply. It is likely that foxes inhabiting a natural area such as Shiretoko NP may begin to beg for provisions simply because they are offered them by the numerous visitors. Provisions may also be a critical food in terms of increasing the carrying capacity of the area normally regulated by natural food availability.

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